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Taxonomy and evolution of the genus *Ocinebrellus* (Gastropoda : Muricidae) in Japan

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Abstract. We have examined the genus- and species-level taxonomy and distribution of the ocenebrine muricid gastropod genus *Ocinebrellus* Jousseaume, 1880. The genus comprises two stocks. . The *O. inornatus* stock includes *O. inornatus* (Recluz, 1851) and *O. lumarius* (Yokoyama, 1926). The *O. aduncus* stock comprises *O. aduncus* (Sowerby, 1834), *O. protoaduncus* (Hatai and Kotaka, 1959) and *O. ogasawarai* sp. nov. Since its first appearance during the middle Miocene, *Ocinebrellus* has been limited to the warm- and cool-temperate shallow seas of northeastern Asia.

Key words : Evolution, Gastropoda, Muricidae, *Ocinebrellus*, Taxonomy

Introduction

The genus *Ocinebrellus* is an endemic ocenebrine muricid group living in shallow warm- to cool-temperate seas in northeastern Asia (Figure 1). It comprises three living species, namely, *Ocinebrellus inornatus* (Recluz), *O. lumarius* (Yokoyama) and *O. aduncus* (Sowerby). Their larvae are non-planktotrophic in development (Amio, 1963).

Among these, *O. inornatus* is a well-known drilling predator of bivalves (Chew and Eisler, 1958) and is the only species in its genus to have been introduced to another part of the world. As reviewed by Carlton (1992), the earliest record of *O. inornatus* on the west coast of North America dates from 1924 in Puget Sound, Washington. Today, the species extends in the northeastern Pacific locally in bays from British Columbia to Morro Bay, California (Carlton, 1992).

Phenotypic variation is so great that the genus- and species-level taxonomy of *Ocinebrellus* has remained confused. This confusion has made it difficult to interpret the fossil record of the group. As a result, no comprehensive account of the living and fossil species of *Ocinebrellus* exists.

Ocinebrellus is one of a number of clades that originated and diversified during the Neogene in warm- to cool-temperate waters of the North Pacific. Whereas the genus has apparently remained confined to the northwestern Pacific, other ocenebrine genera such as *Nucella* have spread throughout the northern hemisphere (Amano *et al*., 1993 ; Collins *et al*., 1996). It would be instructive to know why the same ocenebrines with a similar non-planktotrophic larval stage have achieved such different geographical distributions.

In this paper, we taxonomically revise the species of *Ocinebrellus*, and outline the evolutionary and biogeographical history of the group in comparison to other Neogene warm- to cool-temperate clades.

Materials and Methods

As part of this study, some fossil specimens were collected by hand from the following formations : Pliocene, Tentokuji Formation, Akita Prefecture, Locality 3 of Amano *et al*. (1996) ; Pliocene, Kuwae Formation, Niigata Prefecture, Locality 2 of Amano (1997a) ; early Pleistocene, Setana Formation, Hokkaido, Locality 2 of Amano (1997b) ; early Pleistocene, Omma Formation, Ishikawa Prefecture, Locality 5 of Amano *et al*. (1996). These specimens are housed in the Joetsu University of Education (JUE).

In addition, we have examined many fossil and Recent specimens, including types, at the following institutions : American Museum of Natural History (AMNH), Academy of Natural Sciences of Philadelphia (ANSP), Tohoku University (IGPS), Saito Ho-on Kai Museum of Natural History (SHM), Museum of University of Tokyo (UMUT) and National Science Museum (NSMT). Konstantin A. Lutaenko (Institute of Marine Biology, Russian Academy of Sciences) and Anton Oleinik (Purdue University) kindly provided Recent specimens from Korea and Russia.

We have measured or evaluated the following characters : shell height, spire height, length of siphonal canal, number and shape of axial ribs or varices on the last whorl, number of spiral cords on the last whorl, number of denticles on the inner (adaxial) side of outer lip, presence of a labral tooth on the abapical sector of the outer lip, condition (open or sealed) of the siphonal canal (see Figure 2).

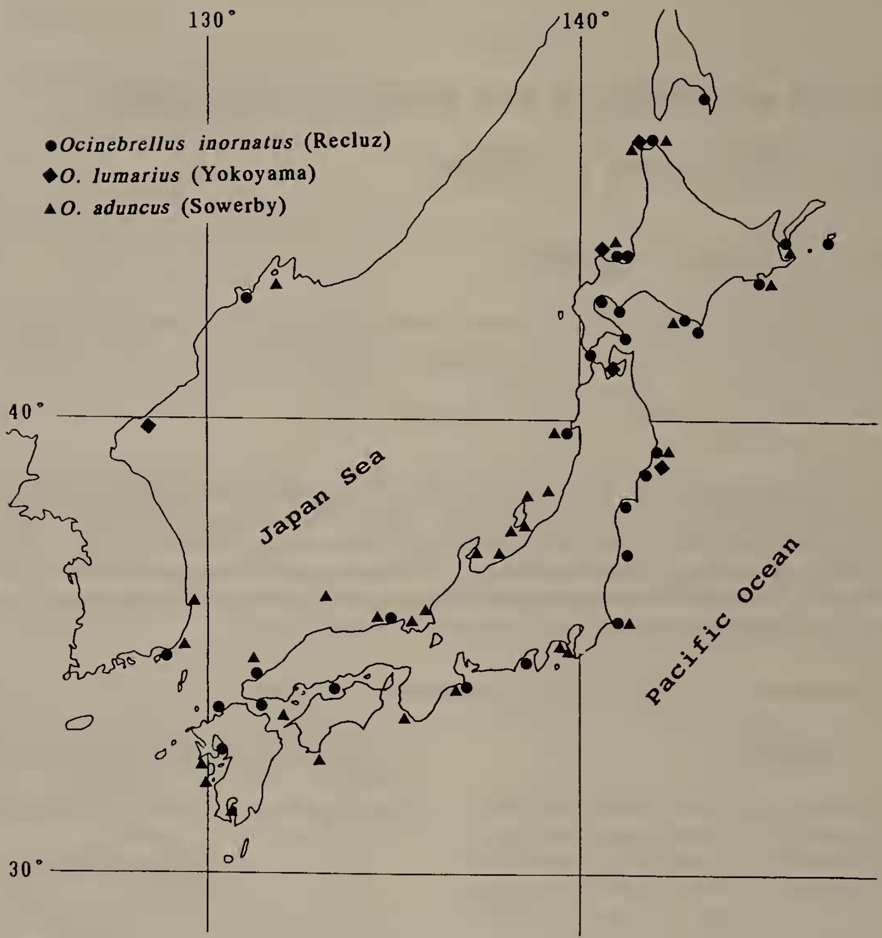


Figure 1. Distribution of the Recent *Ocinebrellus* (mainly after the collection stored in National Science Museum, Tokyo as well as our collections).

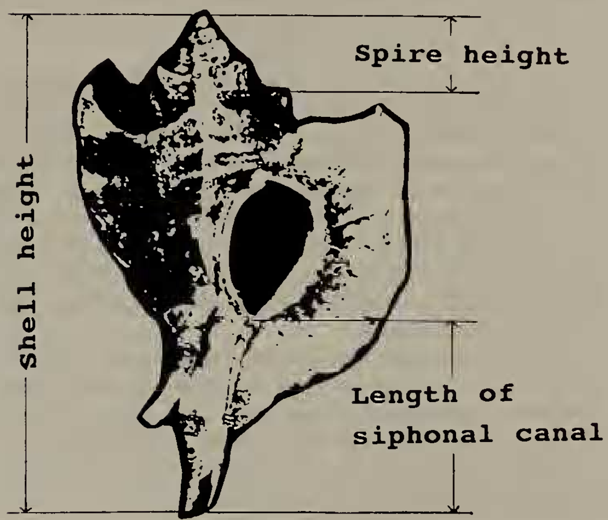


Figure 2. Measurement position.

Systematics

Family Muricidae Rafinesque, 1815
Subfamily Ocenebrinae Cossmann, 1903

Remarks.—The muricid subfamily Ocenebrinae comprises a large number of genera, which are mainly known from the Oligocene to the Recent. One group, which includes *Ocinebrellus*, is characterized by a ventrally (adaperturally) sealed siphonal canal in the adult shell, and by the predominance of axial over spiral sculpture on postnuclear whorls. Vermeij (1998, *in press*) has provided a key to all ocenebrine genera with a sealed siphonal canal.

Genus ***Ocinebrellus*** Jousseaume, 1880

Type species.—*Murex eurypteron* Reeve, 1845 by original designation, = *Murex aduncus* Sowerby, 1834.

Remarks.—Jousseaume (1880, p. 335) introduced *Ocinebrellus* as a new genus in a list of Purpuridae (=Muricidae). In a later paper (Jousseaume, 1882, p. 331), he provided a brief diagnosis for the genus, as well as a list of included species. Jousseaume (1882) characterized *Ocinebrellus* as having four wing-like varices extending abapically to the middle of the sealed canal. Besides the type species, he included *Murex aduncus* Sowerby, *M. falcatus* Sowerby, and *M. acanthophorous* (A. Adams) in the genus. All these taxa are here considered synonymous of a single species for which the oldest available name is *Murex aduncus* Sowerby, 1834 (see also Fulton, 1917). Curiously, Jousseaume (1882) assigned *Murex inornatus* Recluz here included in the genus *Ocinebrellus* and *M. talienwhanensis* Crosse (a synonym of *M. inornatus*) to *Crassilabrum* Jousseaume, 1880, a genus otherwise endemic to southwestern South America. Based on our examination of all species in the genus, we offer the following revised diagnosis of *Ocinebrellus*.

Revised diagnosis.—Shell of small to medium size, maximum height approximately 60 mm; protoconch paucispiral, consistent with nonplanktotrophic development; teleoconch whorls strongly shouldered; four to five in number; last whorl basally constricted, large. Axial sculpture of last whorl consisting of three to twelve varices or axial ribs, which are strongly angulated and often spinose at the periphery and which may be adaperturally reflected; spiral sculpture of last whorl usually consisting of four principal cords which form waves or spines on the varices or ribs, and a variable number of intercalated threads. Outer lip is planar, often with five to nine small denticles on its inner (adaxial) side; small labral tooth occasionally present on edge of outer lip below fourth principal spiral cord at upper end of siphonal canal; adapical end of inner lip without parietal tooth or rib; siphonal canal usually ventrally (adapertually) sealed.

Variability.—Several characters are variably expressed in *Ocinebrellus*. Axial sculpture may consist of simple ribs of uniform size, or it may be differentiated into large varices extending onto the upper end of the siphonal canal and shorter, long ribs. If varices are present, they typically occur on late growth stages of larger shells. Varices are more typical of the *O. aduncus* group than of the *O. inornatus* group (see below). The outer lip of *Ocinebrellus* is characterized abapically by a very short labral tooth in some individuals, especially in larger specimens of *O. aduncus* and *O. inornatus*; but in other specimens there is no trace of the tooth. The adapical sector of the outer lip above the shoulder forms a distinct shallow sinus in *O. inornatus*, but not in *O. aduncus*. Denticles may be present in some individuals of *Ocinebrellus*, but their degree of expression varies considerably, and in many specimens they are absent. Finally, although the siphonal canal is sealed in most individuals, it occasionally remains ventrally open.

Comparison.—*Ocinebrellus* is most similar in shell characters to the genera *Ceratostoma* Herrmannsen, 1846; *Pteropurpura* Jousseaume, 1880; *Muregina* Vermeij, 1998 *in press*; and *Pterorytis* Conrad, 1863 (for additional discussion *see* Vermeij, 1998 *in press*).

Ceratostoma usually has three (rarely four) varices on the last whorl. These are typically blade-like rather than recurved, and lack a spine-like projection at the shoulder as is typical of *Ocinebrellus*. Adjacent varices in *Ceratostoma* are separated by a short axial node. The labral tooth of *Ceratostoma* is almost always well developed, and is usually spine-like.

Pteropurpura, like *Ceratostoma*, has three varices on each adult whorl, adjacent ones being separated by a short intervarical node. The varices are usually blade-like, but may be strongly abapertually reflected, as in *P. festiva* (Hinds). The varices in *Pteropurpura* are not usually spinose at the shoulder or periphery. In *Poropteron* Jousseaume, 1880 (South Africa) and *Calcitrapessa* Berry, 1959 (Baja California, Mexico), two genera closely similar to *Pteropurpura*, the varices are adapically extended as adaperturally and adapically pointing spines respectively. There is no labral tooth in *Pteropurpura, Poropteron* and *Calcitrapessa*.

The tropical eastern Pacific genus *Muregina* resembles *Ocinebrellus* in having four principal cords on the last whorl and in having a labral tooth. It differs from *Ocinebrellus* by having all axial elements of the same size, and by usually lacking a peripheral angulation on the axial sculpture.

Pterorytis Conrad, 1863 differs from *Ocinebrellus* in having only three instead of four principal cords on the last whorl, of which the upper one forms a strong keel connecting the well-developed, often abaperturally reflected varices. In *Pterorytis*, the varices are not angulated at the periphery as they are in *Ocinebrellus*. A long, spine-like labral tooth is usually present in *Pterorytis* (Vermeij and Vokes, 1997).

Finally, the genus *Ocenebra* Gray, 1847, as restricted by Vermeij and Vokes (1997), is an eastern Atlantic group characterized by eight or more strong principal spiral cords and by the absence of a labral tooth. Axial sculpture of *Ocenebra* is variably developed, sometimes consisting of three varices on the last whorl separated by a narrower intervarical rib, and sometimes consisting of axial ribs of similar size.

Ocinebrellus inornatus (Recluz, 1851)

Figures 3—4, 5, 7-10, 15

Murex inornatus Recluz, 1851, p. 207-209, pl. 6, fig. 8; Sowerby, 1879, fig. 234.
Murex crassus A. Adams, 1853, p. 269.
Murex japonicus Dunker, 1860, p. 4, pl. 1, fig. 14.
Murex talienwhanensis Crosse, 1862, p. 56-57, pl. 1, fig. 9.
Murex endermonis Smith, 1875, p. 420; Sowerby, 1879, fig. 213.
Murex (Ocinebra) inornatus Recluz, Tryon, 1880, p. 126-127, pl. 37, fig. 444.
Murex (Ocinebra) japonicus Dunker. Tryon, 1880, p. 126, pl. 37, figs. 445-448.
Murex (Ocinebra) endermonis Smith. Tryon, 1880, p. 128, pl. 38, fig. 454.
Murex polygonulus Lamarck. Yokoyama, 1931, p. 200-201, pl. 12, figs. 3a, b.
Tritonalia inornata endermonis (Smith). Kinoshita and Isahaya, 1934, pl. 5, fig. 36.
Tritonalia inornata (Recluz). Kuroda, 1931, p. 86, pl. 10, fig. 81; Nomura and Hatai, 1936, p. 140-141, pl. 17, fig. 5; Egorov, 1992, p. 64, fig. 1-E, (*non* figs. 1C, D, F).
Ocenebra japonica endermonis (Smith). Kira, 1959, p. 60, pl. 24, fig. 1.
Ocenebra japonica (Dunker). Kira, 1959, p. 60, pl. 24, fig. 7; Habe, 1958, p. 19-20, pl. 3, figs. 8, 11; Habe, 1961, pl. 4, fig.

10; Habe and Ito, 1965, p. 38, pl. 11, figs. 6, 7; Iwai and Shiobara, 1968, pl. 3, figs. 11a, b; Yoo, 1976, p. 72, pl. 12, figs. 8-10; Akamatsu, 1980, p. 6-7, pl. 1, fig. 10; Akamatsu, 1984, p. 9, pl. 1, fig. 19; Ogasawara *et al.*, 1986, pl. 68, fig. 9; Baba, 1990, p. 154-155, pl. 9, fig. 9; Noda *et al.*, 1993, p. 178, pl. 26, figs. 7a, b, pl. 27, figs. 1a-4b; Amano and Sato, 1995, figs. 5, 6.

Ocenebra endermonis (Smith). Habe and Ito, 1965, p. 39, pl. 11, fig. 8; Iwai and Shiobara, 1968, pl. 3, figs. 12a, b; Ogasawara *et al.*, 1986, pl. 69, fig. 21.

Ceratostoma cf. *aduncum* (Sowerby). Iwai and Shiobara, 1968, pl. 3, fig. 10.

Ocenebra cf. *japonica* (Dunker). Iwasaki, 1970, p. 419-420, pl. 5, figs. 10, 11.

Ceratostoma inornatum (Recluz). Radwin and D'Attilio, 1976, p. 113, pl. 18, figs. 10-12.

Tritonalia japonica (Dunker). Golikov and Kusakin, 1978, p. 200-201, fig. 138.

Ceratosoma (*Ocenebra*) *japonica* (Dunker). Tsuchida, 1991, p. 3, pl. 1, figs. 7, 8.

Type Locality.—Korea (exact locality is unknown).

Material.—Twenty-eight Recent and fossil specimens.

Remarks.—The shell of *Ocinebrellus inornatus* is medium-sized, maximum height 47.9 mm, fusiform, solid, and with low spire (spire height : shell height = 0.21-0.29). Protoconch whorls are small and smooth. There are five teleoconch whorls. The last whorl is sculptured with four to twelve (commonly eight to nine) axial ribs or varices, which are often slightly adaperturally reflected and which are angulated at periphery or shoulder. Spiral sculpture on the last whorl consists of four to seven cords with a few intercalated threads. Above the first cords, there is a narrow subsutural area, corresponding on the outer lip with shallow adapical sinus. The inner (adaxial) side of outer lip usually bears five small denticles. A short labral tooth occasionally present below the fourth principal cord. Siphonal canal short (canal length : shell height = 0.22-0.31) and may occasionally be open.

Most Japanese authors used the specific name *Ocenebra japonica* (Dunker) for a species known in Japanese by the name ouu-youraku, which lacks a labral tooth; and the name *O. endermonis* for the so-called ezo-youraku, characterized by the presence of a labral tooth. We cannot discern any consistent differences between the *O. japonica* and *O. endermonis* phenotypes other than the presence or absence of the labral tooth. Specimens with and without a labral tooth co-occur at many sites, including Cape Arutori (Hokkaido), Muroran (Hokkaido; type locality for *Murex endermonis*) and Posiet Bay (Primorie). The same phenotypes can be observed in the artificially introduced population in Hood Canal (Washington) (AMNH no. 123802) and Bellingham Bay (Washington) (AMNH no. 140079). Therefore, as already pointed out by Nomura and Hatai (1935a), the *O. japonica* and *O. endermonis* phenotypes belong to the same species, for which the oldest name is *Murex inornatus*.

Radwin and D'Attilio (1976) placed *Ocenebra monoptera* Pilsbry, 1904, in synonymy with *Ocinebrellus inornatus*. The description and illustration of this species (Pilsbry, 1904, p. 17, plate 5, figs. 32, 32a) and our examination of the type material (ANSP 86123) show that *O. monoptera* is not conspecific with *Ocinebrellus inornatus* and that it is, in fact, not even a member of the genus *Ocinebrellus*. This small species (height 12 mm) is characterized by a single very broad, blade-like terminal varix, a strongly erect outer lip whose edge extends distinctly beyond the adapertural face of the varix, and ten to eleven low, sharply rounded axial ribs that on the last whorl extend neither to the suture nor to the strongly constricted base. The subsutural area is smooth. From the rounded shoulder to the tip of the ventrally sealed canal, there are about eleven fine primary spiral cords, of which three are visible on the penultimate whorl. The species appears to belong to the Ocenebrinae, but we do not know to which genus it should be assigned.

Comparisons.—*Ocinebrellus inornatus* is most similar to *O. lumarius* (Yokoyama) in having a short siphonal canal, a similar number of axial ribs on the last whorl (six to eleven), and five or six denticles on the inner side of the outer lip. *O. inornatus* differs from *O. lumarius* by being larger, having a lower spire, and by occasionally having a labral tooth.

Distribution.—Miocene to Recent. Miocene: Kubota Formation, Fukushima Prefecture. Pliocene: Kume Formation, Ibaraki Prefecture; Nadachi Formation, Niigata Prefecture; Takafu and Joshita Formations, Nagano Prefecture. Pleistocene: Shimonopporo and Zaimokuzawa Formations, Hokkaido; Noheji Formation, Amomori Prefecture; Shibikawa Formation, Akita Prefecture; Kiwada and Mandano Formations in Chiba Prefecture. Recent: Busse Lagoon, Sakhalin; off Kunashiri and Shikotan, Kurile Islands; Hokkaido to Kyushu; Korea; Posiet Bay, Primorie; Bohai Bay, China; British Columbia to Morro Bay (artificially introduced).

Figure 3. **1-3, 6**: *Ocinebrellus lumarius* (Yokoyama). 1a, b; ×1.2, JUE no. 15640, Setana Formation. 2a, b; ×1.2, NSMT-Mo no. 49546, Asamushi (Recent). 3a, b; ×1.5, UMUT CM no. 23118, Holotype, Sawane Formation. 6a, b; ×1.2, SHM no. 6146, Daishaka Formation. **4-5, 7-10, 15**: *Ocinebrellus inornatus* (Recluz). 4a, b; ×1, JUE no. 15641, Cape Erimo (Recent). 5; ×1, JUE no. 15642, Akkeshi (Recent). 7a, b; ×1, IGPS no. 94814, Koje Do Is., Korea (Recent). 8; ×1, UMUT CM no. 9358, "*Ocenebra* cf. *japonica* (Dunker)" by Iwasaki (1970), Kubota Formation. 9a, b; ×1.2, UMUT CM no. 25896, "*Murex polygonulus* Lamarck" by Yokoyama (1931), Kubota Formation. 10a, b; ×1, SHM no. 2672, "*Tritonalia inornata* (Recluz)" by Nomura and Hatai (1936), Kubota Formation. 15a, b; ×1, NSMT-Mo no. 49538, Toba (Recent). **11a, b**: "*Ocenebra*" *katayamai* Matsubara; 11a, ×1.5, 11b, ×1, IGPS no. 102629, Holotype, Yotsuyaku Formation. **12-14**: *Ocinebrellus ogasawarai* sp. nov. 12; ×1.2, JUE no. 15643, Kuwae Formation. 13a, b; ×1, JUE no. 15635, Holotype, Omma Formation. 14a, b; ×1, UMUT CM no. 12783, "*Tritonalia* (*Ocinebrellus*) *adunca* (Sowerby) subsp. by Otuka (1936), Sasaoka Formation. **16a, b**: *Ocinebrellus protoaduncus* (Hatai and Kotaka), ×1, IGPS no. 77798, Holotype, Ginzan Formation.


1a
2a
3a
3b
2b
1b
4a
4b
5
6a
6b
9b
9a
8
14a
7a
7b
11a
12
13a
13b
10a
10b
11b
14b
15a
15b
16a
16b

Ocinebrellus lumarius (Yokoyama, 1926)

Figures 3—1-3, 6

Ocinebra lumaria Yokoyama, 1926, p. 270, pl. 32, fig. 21.
Tritonalia inornata lumaria (Yokoyama). Kinoshita and Isahaya, 1934, p. 8, pl. 5, fig. 37.
Tritonalia lumaria (Yokoyama). Nomura and Hatai, 1935b, p. 124-125, pl. 13, figs. 1a, b.
Ocenebra lumaria (Yokoyama). Habe and Ito, 1965, p. 38, pl. 11, fig. 2.
Ceratostoma sp., Iwai, 1965, pl. 20, fig. 15.
Ceratostoma (*Ocenebra*) *japonicum* (Dunker). Matsuura, 1977, pl. 1, fig. 33.
Ceratostoma (*Ocenebra*) *lumaria* Yokoyama. Tsuchida, 1991, p. 3, pl. 1, figs. 5, 6.

Type locality.—Sawane in Sado Island of Niigata Prefecture.

Type specimen.—UMUT CM no. 23118 (Holotype).

Material.—Thirty-three Recent and fossil specimens.

Remarks and comparisons.—This is the smallest species of *Ocinebrellus*, with a maximum shell height of 23.1 mm. The shell is fusiform, slender, and high-spired, with a spire height : shell height ratio of 0.27 to 0.33. Two small, smooth protoconch whorls are followed by six teleoconch whorls. The body whorl is sculptured by six to eleven (usually six to eight) axial ribs or varices, which are pointed at the periphery. These are crossed by twelve to twenty spiral cords. The terminal varix is extended to the most basal portion of the last whorl. A narrow subsutural area above the shoulder is sculptured by one spiral cord. The outer lip usually has five to six small denticles on its inner side; a labral tooth is absent. The siphonal canal is short (canal length : shell height = 0.16 to 0.26) and usually sealed, but is occasionally open.

Kinoshita and Isahaya (1934) considered *O. lumarius* a subspecies of *O. inornatus*, whereas Radwin and D'Attilio (1976) regarded the two taxa as synonyms. Because *O. lumarius* differs consistently from *O. inornatus* and both species have been recorded from Otuchi Bay in Iwate Prefecture (Tsuchida, 1991), we regard the two taxa as separate, distinct species. *O. lumarius* is smaller than *O. inornatus* with the same number of teleoconch whorls. Moreover, *O. lumarius* has a higher spire and more numerous spiral cords (twelve to twenty instead of four to seven) on the last whorl. Habe and Ito (1965) pointed out that *O. lumarius* resembles young individuals of *O. inornatus*. It is therefore probable that *O. lumarius* is phylogenetically derived from the larger *O. inornatus*.

Distribution.—Pleistocene to Recent. Pleistocene: Sawane Formation, Niigata Prefecture; Setana Formation, Hokkaido; Daishaka Formation, Aomori Prefecture; Uji Shell-bed, Ishikawa Prefecture. Recent: Wakkanai, Oshoro and Takashima, Hokkaido; Asamushi, Aomori Prefecture; Otsuchi Bay, Iwate Prefecture; Shinpo, North Korea.

Ocinebrellus protoaduncus (Hatai and Kotaka, 1959)

Figures 3—16a, b

Ocenebra adunca protoadunca Hatai and Kotaka, 1959, p. 10, figs. 1, 3.

Type locality.—Upstream of Okama-zawa, Obanazawa City, Yamagata Prefecture.

Type specimen.—IGPS no. 77798 (Monotype).

Remarks and comparison.—This species is known from a single specimen, characterized by seven varices which are less spinose at the periphery than in most *Ocinebrellus aduncus*. There are four strong spiral cords on the last whorl, and seven denticles on the inner side of the outer lip. The siphonal canal is sealed. A labral tooth is absent. The varices are neither pointed nor reflected, but instead are blade-like, as in *Ceratostoma*. The four cords are stronger than those in *O. aduncus*.

Measurements (*in mm*).—

Specimen	Height	Spire height	Canal length
IGPS no. 77798 (Holotype)	44.6+	10.1	10.3+

Distribution.—Miocene Ginzan Formation in Yamagata Prefecture.

Ocinebrellus ogasawarai sp. nov.

Figures 3—12-14; 4—1, 4-6, 9, 13

Tritonalia (*Ocinebrellus*) *adunca* (Sowerby) subsp. Otuka, 1936, p. 733-734, pl. 42, figs. 15a, b (*non* figs. 9, 13).
Ceratostoma (*Ocenebra*) *japonica* (Dunker). Kaseno and Matsuura, 1965, pl. 3, figs. 6-8; Matsuura, 1985, pl. 38, fig. 11.
Ocenebra aduncum (Sowerby). Ogasawara, 1977, p. 134-135, pl. 19, figs. 8, 11-13, 15, 17.
Ocenebra japonica (Dunker). Ogasawara *et al*., 1986, pl. 23, fig. 10.

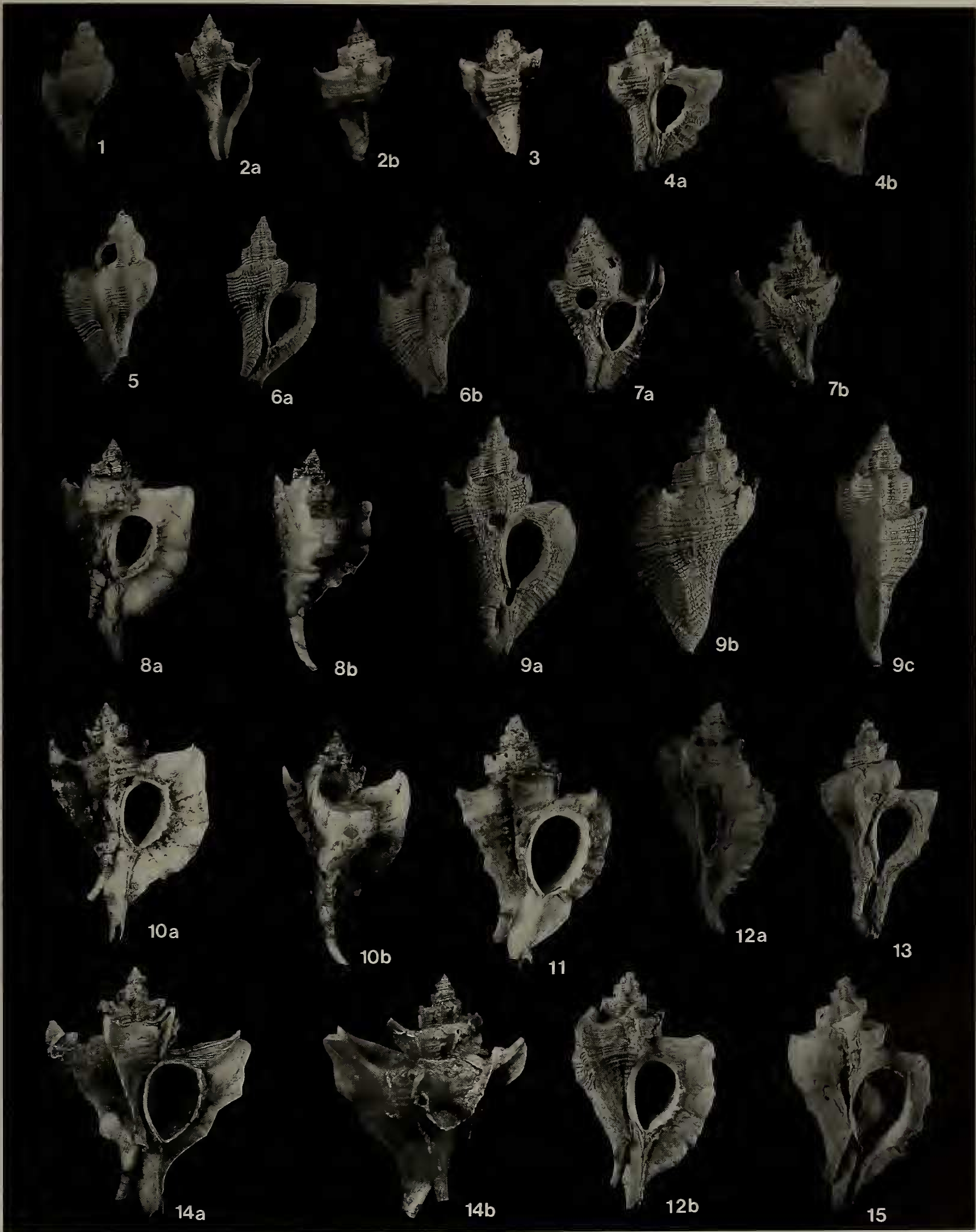
Type Locality.—Bank of Sai River, early Pleistocene Omma Formation.

Type Specimens.—JUE no. 15635 (Holotype), 15636, 15637, 15638 (Paratypes).

Material.—Thirteen fossil specimens.

Diagnosis.—Medium-sized ocenebrine shell characterized by numerous spiral cords (eighteen to forty-four on last whorl), three to ten axial ribs or varices on body whorl,

Figure 4. **1, 4-6, 9, 13**: *Ocinebrellus ogasawarai* sp. nov. 1; ×1.2, JUE no. 15644, Tentokuji Formation. 4a, b; ×1, JUE no. 15639-1, Omma Formation. 5; ×1.2, JUE no. 15639-2, Omma Formation. 6a, b; ×1.25, JUE no. 15637, Paratype, Omma Formation. 9a-c; ×1.5, JUE no. 15636, Paratype, Omma Formation. 13; ×1.5, JUE no. 15638, Paratype, Omma Formation. **2, 3, 7, 8, 10-12, 14, 15**: *Ocinebrellus aduncus* (Sowerby). 2a, b, 8a, b, 10a, b; ×1, NSMT-Mo no. 60254, Oshoro (Recent). 3; ×1, SHM no. 2192, Tatsunokuchi Formation. 7a, b; ×1.5, UMUT CM no.12784a, Semata Formation. 11; ×1, JUE no. 15645, Pohang, Korea (Recent). 12a, b; ×1, JUE no. 15646, Peter the Great Bay, Russia (Recent). 14a, b; ×1, NSMT-Mo no. 46277, "*Murex eurypteron* Reeve" type, Tosa (Recent). 15; ×1, JUE no. 15647, off Cape Erimo (Recent).


1
2a
2b
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7b
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10b
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12b
15

denticulated inner side of outer lip and long sealed siphonal canal.

Description.—Shell of medium size, fusiform, with a low spire; protoconch of two smooth whorls; teleoconch of five whorls. Axial sculpture consisting of six to seven ribs or varices on the penultimate whorl, and three to ten (usually six to seven) ribs or varices on the body whorl; axial elements pointed at periphery; spiral sculpture consisting of two to sixteen cords on the penultimate whorl, and eighteen to forty-four cords on the body whorl; cords mostly of equal size except for a strong keel just above periphery. Suture impressed, distinct; flattened subsutural area above keel ornamented with three spiral cords. Aperture ovate, rather large; inner side of outer lip with five to nine (commonly seven) denticles; labral tooth absent; siphonal canal long, sealed.

Remarks and comparisons.—The new species *Ocinebrellus ogasawarai* is restricted to the Pliocene and early Pleistocene of the Japan Sea borderland. As indicated in the synonymy, *Ocinebrellus ogasawarai* was previously confused with *O. aduncus* (Ogasawara, 1977) and *O. inornatus* (as *O. japonica*) (Kaseno and Matsuura, 1965; Matsuura, 1985; Ogasawara *et al.*, 1986). Otuka (1936) identified it as an unnamed subspecies of *Ocinebrellus aduncus*.

Ocinebrellus ogasawarai resembles *O. aduncus* (Sowerby) in its low spire (spire height : shell height = 0.20 to 0.30), long siphonal canal (canal length : shell height = 0.33 to 0.36), and similar number of axial ribs (three to ten on the body whorl). The presence of denticles on the inner side of the outer lip distinguishes *O. ogasawarai* from *O. aduncus*. A few Recent specimens of *O. aduncus* from off Cape Erimo (Hokkaido) and Peter the Great Bay (Primorie) occasionally have very weak denticles. The new species differs from *O. aduncus* in addition by having more numerous spiral cords on the last whorl (eighteen to forty-four instead of one to twenty), by having the axial ribs usually not reflected, and in the absence of a labral tooth.

O. protoaduncus resembles the new species in having a similar number of axial ribs and in possessing denticles on the inner side of the outer lip, but *O. protoaduncus* has fewer cords and does not have the pointed axial varices.

Measurements (in mm).—

Specimens	Height	Spire height	Canal length
JUE no. 15635 (Holotype)	38.7+	9.7	12.6
JUE no. 15636 (Paratype)	29.4	8.7	10.4
JUE no. 15637 (Paratype)	25.8	6.3	6.4
JUE no. 15638 (Paratype)	33.1	7.1	11.7

Distribution.—Pliocene to early Pleistocene. Pliocene: Tentokuji and Sasaoka Formations, Akita Prefecture; Kuwae Formation, Niigata Prefecture; Zukawa Formation, Toyama Prefecture. Early Pleistocene: Omma Formation, Ishikawa Prefecture.

Etymology.—This species is named after Prof. Kenshiro Ogasawara of the Univeristy of Tsukuba, who studied the Omma fauna in detail and suggested that the Omma population possesses a wide range of variation.

Ocinebrellus aduncus (Sowerby, 1834)

Figures 4—2, 3, 7, 8, 10-12, 14, 15

Murex aduncus Sowerby, 1834, pl. 62, fig. 35; Sowerby, 1879, p. 45, fig. 216.
Murex falcatus Sowerby, 1834, pl. 62, fig. 31; Sowerby, 1979, p. 44-45, fig. 149; Tokunaga, 1906, p. 4, pl. 1, fig. 1.
Murex eurypteron Reeve, 1845, figs. 176a, b; Sowerby, 1879, p. 25, fig. 106.
Murex speciosus A. Adams, 1855, p. 121.
Murex expansus Sowerby, 1859, p. 428, fig 5.
Phyllonotus acanthophorous A. Adams, 1862, p. 372.
Murex (Ocinebra) falcatus Sowerby. Tryon, 1880, p. 127, pl. 38, figs. 457-459.
Ocinebra falcata (Sowerby). Yokoyama, 1922, p. 65, pl. 3, fig. 4.
Ocinebra spectata Yokoyama, 1922, p. 65-66, pl. 3, fig. 5.
Tritonalia (Ocinebrellus) adunca (Sowerby). Kinoshita and Isahaya, 1934, p. 8, pl. 5, fig. 39.
Tritonalia (Ocinebrellus) adunca (Sowerby) subsp. Otuka, 1936, pl. 42, figs. 9a, b, 13, 14 (*non* fig. 15).
Tritonalia adunca (Sowerby). Nomura, 1938, p. 269, pl. 34, fig. 19; Kanehara, 1942, pl. 3, figs. 8a-b.
Ocenebra (Ocinebrellus) adunca (Sowerby). Habe, 1958, p. 19, pl. 3, fig. 13, pl. 4, fig. 13; Kira, 1959, p. 60-61, pl. 24, fig. 16.
Ocenebra eurypteron (Adams and Reeve). Kira, 1959, p. 61, pl. 24, fig. 16.
Ceratostoma (Ocenebra) aduncum (Sowerby). Hatai *et al.*, 1961, pl. 3, fig. 6; Tsuchida, 1991, p. 3, pl. 1, figs. 9, 10.
Ocenebra adunca (Sowerby). Habe and Ito, 1965, p. 38, pl. 11, figs. 3, 4; Baba, 1990, p. 154, pl. 9, figs. 8a-b.
Ocinebrellus aduncus (Sowerby). Hall, 1959, p. 432-433, pl. 2, figs. 1-3; Kuroda *et al.*, 1971, p. 147-148, pl. 40, figs. 3-5; Ito *et al.*, 1986, pl. 10, fig. 4; Ito, 1989, pl. 6, fig. 2.
Ocenebrellus falcatus (Sowerby). Yoo, 1976, p. 71, pl. 12, fig. 5.
Ocenebrellus adunca (Sowerby). Yoo, 1976, p. 73, pl. 13, figs. 6, 7.
Pteropurpura adunca (Sowerby). Radwin and D'Attilio, 1976, p. 129, pl. 22, fig. 10.
? *Ocenebra japonica* (Dunker). Nemoto and O'Hara, 1979, pl. 1, fig. 13.
Ceratostoma aduncum (Sowerby). Ogasawara *et al.*, 1986, pl. 68, figs. 7, 12, 16.
Ocinebrellus falcatus eurypteron (Adams and Reeve). Ito *et al.*, 1986, pl. 10, fig. 3.
? *Ocenebrellus* sp., Takahashi, 1986, pl. 14, figs. 15a-b.

Type Locality.—Japan (exact locality is unknown).

Material.—Seventy-five Recent and fossil specimens.

Remarks.—This species is characterized by a large shell (maximum shell height 58.9 mm) with a low spire (spire height : shell height = 0.18 to 0.26) and a long siphonal canal (canal length : shell height = 0.28 to 0.42). The protoconch is small and smooth, and there are six teleoconch whorls. The last whorl is sculptured with three to seven (commonly five) varices, which are usually pointed or spinose at the periphery, and which are frequently adaperturally reflected. Spiral sculpture on the last whorl is highly variable, consisting of one to twenty cords. The flat subsutural area above the first primary cords is smooth. The inner side of the outer lip is usually smooth, but rarely bears very week denticles. Previous authors have not mentioned a labral tooth, but several Recent populations from Hokkaido and Kyushu have a very short labral tooth below the basalmost of the four primary cords.

Murex falcatus has sometimes been distinguished from *M. aduncus* by having the spiral sculpture of the last whorl reduced to a single shoulder keel. *Murex eurypteron* was differentiated from *M. aduncus* by having strongly projecting varices. Radwin and D'Attilio (1976) pointed out, however, that the number and expression of spiral and axial sculptural elements vary greatly both within and between populations. The *M. eurypteron* phenotype may be common in deep water (Kira, 1959), but we see no reason to separate either the *M. eurypteron* or the *M. falcatus* phenotypes from *Ocinebrellus aduncus*.

Comparison.—*Ocinebrellus aduncus* closely resembles *O. ogasawarai* sp. nov. (see above), but differs from that fossil species by having fewer spiral cords, usually lacking denticles on the inner side of the outer lip, and occasionally having a short labral tooth. *Ocinebrellus aduncus* differs from *O. inornatus* by its longer siphonal canal, fewer and more distinct varices, usual absence of denticles on the inner side of the outer lip, and absence of a distinct adapical sinus on the outer lip.

Distribution.—Pliocene to Recent. Pliocene: Tatsunokuchi Formation, Miyagi Prefecture; Tomioka Formation, Fukushima Prefecture; ?Kume Formation, Ibaraki Prefecture. Pleistocene: Hamada Formation, Aomori Prefecture; Shibikawa Formation, Akita Prefecture; Higashi-higasa, Nagahama, Mandano, Semata, Narita Formations, Chiba Prefecture; Koshiba Formation, Kanagawa Prefecture. Recent: Hokkaido to Kyushu, Korea, Peter the Great Bay (Primorie), Bohai Bay (China).

Related or Doubtful Species

In addition to the above species of the genus *Ocinebrellus*, there are several Miocene species whose relationship with *Ocinebrellus* remain uncertain. We treat one of these species as "*Ocenebra*" *katayamai* from the early Miocene Yotsuyaku Formation, in detail, and redescribe this form.

In addition, eight species from the Miocene of Kamchatka described by Sinelnikova in Gladenkov and Sinelnikova (1990) are based on poorly preserved material. We treat these eight species collectively, and are unable to resolve their status.

"***Ocenebra***" ***katayamai*** Matsubara, 1996

Figures 3—11a, b

Type locality.—Upper reaches of the Nesori River about 3 km east of Nosokei, Ichinohe Town, Ninohe County, Iwate Prefecture.

Type specimens.—IGPS no. 102629 (Holotype), 102630, 102631 (Paratypes).

Description.—Shell small, maximum height 29.3 mm; shell thin, fusiform, with a low spire (spire height : shell height = 0.19 to 0.22); protoconch missing, teleoconch consisting four whorls. Last whorl sculptured by seven to eight axial ribs becoming obsolete near aperture; spiral sculpture of body whorl consisting of six to nine low cords separated by secondary and two tertiary threads; strongest spiral cord located at shoulder. Small labral tooth formed at end of fifth spiral cord counting from suture; inner side of outer lip bearing nine small denticles; siphonal canal short (canal length : shell height = 0.21), open.

Remarks and comparison.—Matsubara (1996) assigned his new species to the genus *Ocenebra* Gray, 1847. The presence of a short labral tooth at the apertural end of a cord, a feature not noted by Matsubara (1996) in his original description, clearly distinguishes "*O.*" *katayamai* from typical members of *Ocenebra*.

"*Ocenebra*" *katayamai* resembles *Ocinebrellus inornatus* in having a short siphonal canal, eight axial ribs on the last whorl, denticles on the inner side of the outer lip, and a small labral tooth. However, the two species differ in the position of the labral tooth. In "*O.*" *katayamai*, the labral tooth is formed at the end of a cord (Figure 3-11a), whereas in *O. inornatus* and *O. aduncus*, it is formed at the end of a shallow groove. There is some resemblance between "*Ocenebra*" *katayamai* and the monotypic late Oligocene genus *Fenolignum* Vermeij and Vokes, 1997, from North Carolina. Both are characterized by a blunt labral tooth at the end of a cord, and by the absence of varices. The siphonal canal of *Fenolignum umbilicatum* Vermeij and Vokes, 1997, however, is sealed instead of open.

From this discussion, it is clear that "*Ocenebra*" *katayamai* does not fit comfortably into any described ocenebrine genus. It may be necessary to establish yet another new ocenebrine genus for this taxon, but we are reluctant to take this step here. We leave "*Ocenebra*" *katayamai* in the genus *Ocenebra* as used in the very broadest sense, but we emphasize that this assignment in no way implies a close relationship to eastern Atlantic members of the genus *Ocenebra*.

Russian species Sinelnikova (in Gladenkov and Sinelnikova, 1990) named eight species of *Tritonalia* from the Miocene of Kamchatka on the basis of poorly preserved material from the Kakert (early middle Miocene) and Etolon (middle Miocene) Formations. The descriptions and illustrations are inadequate for robust taxonomic conclusions to be drawn. Several species, such as *T. chejsliensis* from the Kakert Formation, and *T. itelmenica* and *T. palanica* from the Etolon Formation appear to have a much higher spire than any species of *Ocinebrellus*, and therefore probably do not belong to that genus.

Other species have a lower spire and could belong to *Ocinebrellus*. These includes *T. kamtchatica* (Kakert Formation), with high varices and low cords; *T. kavranensis* (Kakert Formation), with sparse varices and low cords; *T. kejtscheensis* (Kakert Formation), with six to seven axial blades and obsolete spiral sculpture; *T. ochotika* (Kakert Formation), with thin axial keels and low broad cords; and *T. rekinicus* (Etolon Formation), with more than ten thin wavy axial varices.

From the figures, *Tritonalia kamtchatica, T. kavranensis* and *T. ochotika* appears to be shouldered as are species of *Ocinebrellus*, whereas *T. rekinicus* is not. The siphonal

Table 1. Species characterers of *Ocinebrellus*.

Species	Characters	Height (mm)	SH/H[1)]	CL/H[2)]	BAN[3)]	BSN[4)]	LT[5)]	NC[6)]	Living depth[7)]	Geologic range
***O. inornatus* Stock**										
O. inornatus (Recluz)		47.9	0.21-0.29	0.22-0.31	4-12	4- 7	+	5	0-20 m	M. Mio.-Rec.
O. lumarius (Yokoyama)		23.1	0.27-0.33	0.16-0.26	6-11	12-20	—	5-6	0-20 m	E. Pleist.-Rec.
***O. aduncus* Stock**										
O. protoaduncus (Hatai and Kotaka)		44.6+	—	—	7	12	—	7	—	M. Mio.
O. ogasawarai sp. nov.		44.3	0.20-0.30	0.33-0.36	3-10	18-44	—	5-9	—	Plio.-E. Pleist.
O. aduncus (Sowerby)		58.9	0.18-0.26	0.28-0.42	3- 7	1-20	+	0	0-200 m	Plio.-Rec.

[1)]SH=spire height [2)]CL=canal length [3)]number of axial varices or ribs on body whorl [4)]number of spiral cords on body whorl [5)]existence of labral tooth [6)]number of denticles on the inner side of outer lip [7)]after Higo and Goto (1993)

canal of *T. kejtscheensis* is apparently sealed, whereas that of seven other species is open. None of the eight species has a labral tooth. It is possible that some of these species belong to *Ocinebrellus*. If so, their early middle Miocene appearance in the Kakert Formation would slightly precede the oldest undoubted species of *Ocinebrellus* from the middle Miocene, *O. protoaduncus* from the Ginzan Formation and *O. inornatus* from the Kubota Formation. Definite resolution of the status and assignment of the eight Russian species of *Tritonalia* must await the discovery of better preserved material.

Evolutionary history

Table 1 provides a summary of the morphology and distribution of the species of *Ocinebrellus*. Morphologically, the genus is divisible into two stocks. In the *O. inornatus* stock, the siphonal canal is typically short and occasionally open, the outer lip has five small denticles on its inner side, an adapical sinus on the outer lip is present, and axial varices are often indistinct or absent. It includes the middle Miocene to Recent *O. inornatus* (Recluz) and the early Pleistocene to Recent *O. lumarius* (Yokoyama).

The *O. aduncus* stock is characterized by a long siphonal canal, seven denticles on the inner side of the outer lip (if present), absence of an adapical sinus, and distinctly developed varices. This stock comprises the middle Miocene *O. protoaduncus* (Hatai and Kotaka), the Pliocene to early Pleistocene *O. ogasawarai* sp. nov., and the Pliocene to Recent *O. aduncus* (Sowerby).

The genus *Ocinebrellus* probably originated in the northwestern Pacific, although its precise origins remain obscure. The early Miocene species "*Ocenebra*" *katayamai* Matsubara may lie close to the ancestry of *Ocinebrellus inornatus*, but as discussed above under "*O.*" *katayamai*, the presence of a labral tooth at the end of a cord instead of at the end of a groove together with the open instead of sealed siphonal canal places "*O.*" *katayamai* outside the genus *Ocinebrellus*.

None of the ocenebrine muricids described from the Miocene of the North American side of the Pacific bears a close resemblance to *Ocinebrellus*. Moore (1963) compared her new species *Ocenebra depoensis* from the Astoria Formation (early middle Miocene) of Oregon to *Ocinebrellus lumarius*, but she noted that *O. depoensis* lacks the shoulder spine characteristic of *Ocinebrellus*. Moreover, the spire of *O. depoensis* is considerably higher. The holotype and only known specimen of *O. depoensis* (USNM no. 563927) has approximately seven denticles on the inner side of the outer lip, approximately seven strong cords on the last whorl, and a high spire. Two of the axial ribs, the one at the outer lip and one ninety degrees back from the aperture, are differentiated as varices. The siphonal canal is sealed. Although the outer lip edge is somewhat damaged, there is no evidence of a labral tooth. This species seems closely related neither to *Ocinebrellus* nor to other North America ocenebrines.

The earliest occurrences of *Ocinebrellus* are in the Miocene strata of northeastern Honshu, which at that time lay in a zone of mild-temperate climate (Ogasawara, 1994). Miocene *Ocinebrellus inornatus* is known from the Kubota Formation in Fukushima Prefecture (Yokoyama, 1931; Nomura and Hatai, 1936; Iwasaki, 1970; Fifures 3-8, 9a, b, 10a, b), while *O. protoaduncus* is recorded from the Ginzan Formation of Yamagata Prefecture (Hatai and Kotaka, 1959; Figure 5). During the Pliocene, *Ocinebrellus aduncus* occurred on the Pacific coast of Honshu, whereas *O. ogasawarai* was restricted to, and probably arose in, the Japan Sea, an enclosed basin dominated by a cold-water fauna (see Ogasawara, 1994). *O. ogasawarai* was found in some mixed Pliocene assemblages of warm shallow and cold deep faunas, and persisted until the end of the early Pleistocene.

During the early Pleistocene, *O. lumarius* was differentiated from *O. inornatus* in the northern part of the Japan Sea. Following the extinction of *O. ogasawarai, O. aduncus* invaded the Japan Sea, where it colonized relatively deep sublittoral habitats.

Recent work has revealed that many gastropods living in the Pliocene and early Pleistocene of Japan Sea suffered extinction at the end of the early Pleistocene. Ogasawara (1986) listed twenty-three shallow-water gastropods in this category, including *Umbonium akitanum* Suzuki, *Turritella saishuensis* (Yokoyama) group, *Trophonopsis kagaensis* Hatai and Nisiyama, *Lirabuccinum japonica* (Yokoyama), *Fulgoraria masudae* Hayasaka, *Ophiodermella ogurana* (Yokoyama). To this list may be added the teleplanicaly dispersed ranellid *Fusitriton izumozakiensis* Amano and *Ranella yasumurai* Amano (see Amano, 1997a). Some deep-water buccinids such as the *Ancistrolepis* group, *Neptunea*, were

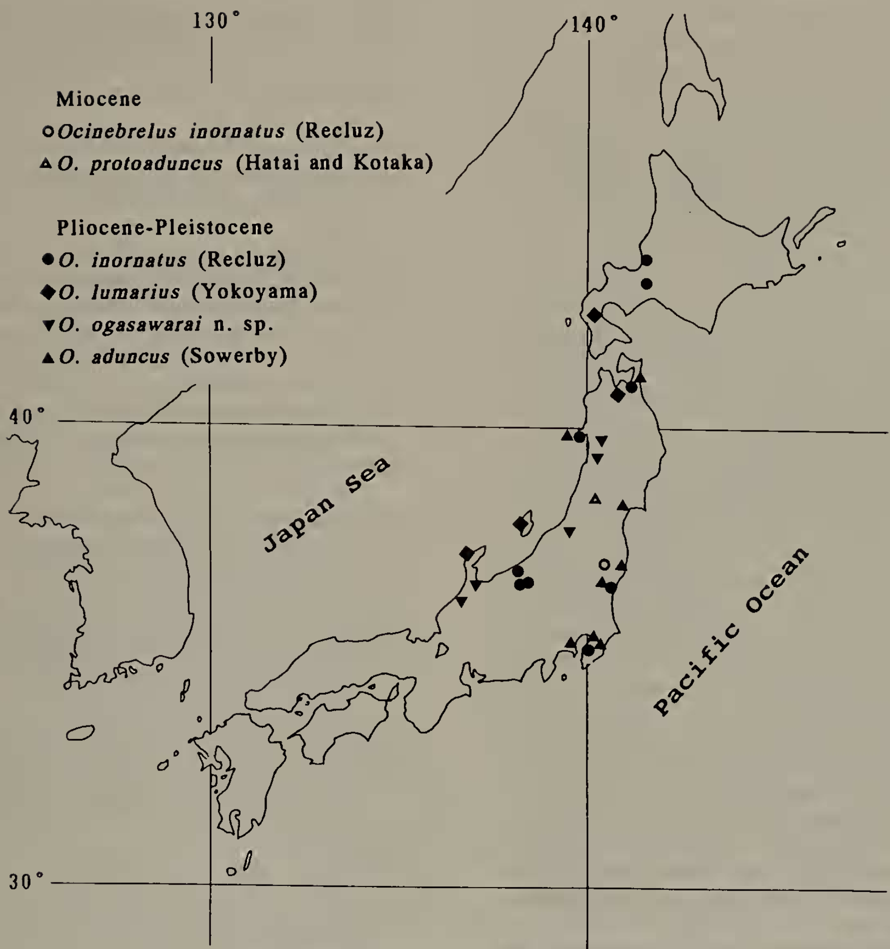

Figure 5. Distribution of fossil *Ocinebrellus*.

also Japan Sea endemics that became extinct at the end of the early Pleistocene (Amano *et al*., 1996; Amano, 1997b). These extinctions probably resulted from the fact that the deep waters of the Japan Sea became euxinic while surface waters became brackish, which in turn resulted from the enclosed nature of the basin during the middle and late Pleistocene glacial low stands of sea level (see Tada, 1994).

Some evolutionary change in *Ocinebrellus* may be related to predation. *O. aduncus* is unusual among species of *Ocinebrellus* in usually lacking denticles on the inner side of the outer lip. Such denticles often have an anti-predatory function (Vermeij, 1987). The paucity of predators in the deep sublittoral habitat of *O. aduncus* is consistent with the absence of denticles in this species.

From the time of its origin, the genus *Ocinebrellus* has been confined to the northwestern Pacific, except for the introduction of *O. inornatus* by humans to the west coast of North America during the first quarter of the twentieth century. This narrow distribution contrasts with that of *Nucella*, another ocenebrine genus. *Nucella* originated during the early Miocene in the warm-temperate north-eastern Pacific, and had expanded westward to Japan and Russia by the early middle Miocene (Amano *et al*., 1993; Collins *et al*., 1996). In the late Pliocene, at least one lineage penetrated into the North Atlantic. Why *Nucella* but not *Ocinebrellus* adapted to boreal water conditions and spread throughout the North Pacific and North Atlantic remains unclear. It is interesting that intertidal species of *Nucella* can easily colonize newly available habitats. In contrast, introduced populations of *Ocinebrellus inornatus* have spread relatively little from their original sites of introduction in western North America (Carlton, 1992). We do not know what accounts for such differences in dispersability. Future evolutionary and comparative biogeographic research on contemporaneous clades should emphasize the means and extent of dispersal in order to make clear why some clades achieve a wide distribution while others evolving at the same time remain confined to a relatively small region.

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